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# MADROÑO

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**Contents**



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# MADROÑO

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# STRUCTURE AND TAXONOMY OF TAENIOMA, INCLUDING A DISCUSSION ON THE PHYLOGENY OF THE CERAMIALES

George F. Papenfuss

The genus *Taenioma* was founded by J. Agardh (2) in 1863 to receive a species which he (1) had previously described as *Polysiphonia perpusilla*. He placed *Taenioma* in the Rhodomelaceae while Schmitz (41) in 1889 included it in his newly created Sarcomenieae, a sub-family of the Delesseriaceae. In conjunction with his monograph on the Rhodomelaceae, Falkenberg (14) also studied *Taenioma* with the specific purpose of demonstrating, by way of contrast, the differences in construction of the thallus between the Rhodomelaceae and Delesseriaceae. The majority of later writers (De Toni, 12, 13; Børgesen, 5, 6; Kylin, 28; and others) who have been concerned with this genus have followed Schmitz and Falkenberg in assigning it to the Delesseriaceae.

Subsequent to the work of Falkenberg, the most important paper on *Taenioma* has been that of Thompson (43) in 1910. Thompson discovered cystocarps for the first time in the genus and from a somewhat superficial study of them concluded that *Taenioma* belonged in the Rhodomelaceae. Recently this view was also adopted by Hollenberg (19). Thompson and Hollenberg, however, overlooked the most significant structural feature distinguishing the Delesseriaceae from the Rhodomelaceae, namely, the difference in the order of formation of the pericentral cells. As was shown by Falkenberg, the pericentral cells in *Taenioma* are formed in the manner characteristic of the Delesseriaceae. This question will be taken up more fully in later pages, after the structure of the thallus has been reviewed.

Kylin (24) in 1923 pointed out that the Sarcomenieae should be united with the Delesserieae, a conclusion borne out by the work of Papenfuss (35) on *Claudea* and *Vanvoorstia*. Knowledge concerning the structure and reproduction of the majority of other genera in this old sub-family is meager. Through the work of Falkenberg (14), Thompson (43), Thuret (9), Børgesen (5) and Okamura (33), *Taenioma* has become one of the better-known members of the Sarcomenieae. Although sexual organs were not present in the writer's material, certain observations on the structure of the thallus and the development of the tetrasporangia seem worthy of record.

The anatomical work in the present study was made on Hawaiian and South African plants of *Taenioma perpusillum*. The South African material was kindly supplied by Dr. Mary A. Pocock who collected it at Arniston (May 7, 1940) and Port Elizabeth (Dec. 8, 1942, with tetrasporangia). The species has been

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reported as occurring in South Africa. The record is based on Kützing's (23) *Polysiphonia nana;* but, as will be pointed out farther on, it is very doubtful if *P. nana* is representative of *Taenioma.* The Hawaiian material was collected by the writer during the years 1940–42 at the following localities on the island of Oahu: Hanauma Bay (March 30, 1941); 1.8 miles northwest of Nanakuli (May 16, 1942, with tetrasporangia); Waikiki (Nov. 17, 1940, and Aug. 21, 1941). Additional Hawaiian material was kindly furnished by Mrs. D. Abbott who obtained it on the ascidian *Pyura momas,* collected by members of the Department of Zoology of the University of Hawaii, at Kaneohe Bay, Oahu (Feb. 11, 1941, with tetrasporangia). All the material collected by the writer was obtained in the intertidal zone, where the species occurs as an epiphyte on *Bornetella* and a variety of small turf-forming algae. *T. perpusillum* had been reported from Hawaii in 1880 by Chamberlain (10) but the record has escaped notice.

The Hawaiian and South African plants seem to be identical in every respect. South African specimens received from Dr. Pocock in 1939, while the writer was working at Lund, were compared with the type material of *T. perpusillum* (nos. 43342 and 43343 in Herb. Agardh) and found to correspond very well. Since only dried South African plants were available for the present study, the following account is based entirely upon observations on Hawaiian material, which was preserved in formalin.

## Structure of Thallus

*Taenioma* is a small alga, measuring less than three millimeters in height, and consisting of a prostrate, terete, branched, indeterminate main axis, attached by non-septate rhizoids on the ventral side and forming erect, terete, secondary indeterminate axes on the dorsal side. According to Falkenberg (14), the erect branches are determinate, but from the writer's observations there seems to be no evidence for this. Both prostrate and erect axes are monopodial and grow by means of a single transversely-dividing initial. The axes are composed of segments consisting of a central and four pericentral cells. The rhizoids arise as outgrowths from the ventral pericentral cells of the prostrate parts. The ascending axes are formed alternately at an interspace of three to eight segments, and by bending upward give the impres-

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Explanation of the Figures. Plate 23.

Plate 23. Taenioma perpusillum. Fig. 1. Portion of thallus showing an erect axis with alternate determinate branches and with indeterminate branches on the adaxial side of the latter, ×125. Fig. 2. Portion of a determinate branch with three young apical hairs, ×600. Fig. 3. Distal ends of determinate branches showing the terminal monosiphonous hairs, ×125. Fig. 4. Basal region of a determinate branch with mature tetrasporangia, ×600.

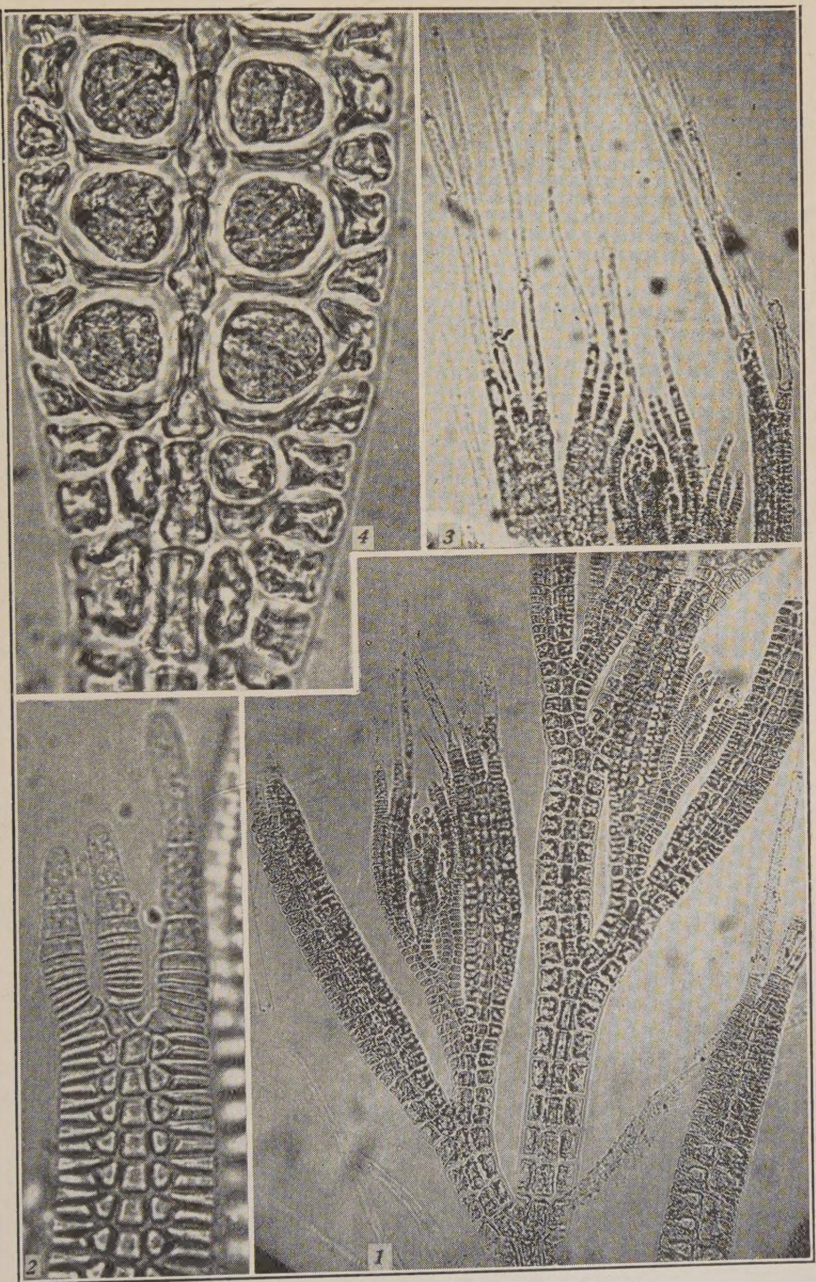


PLATE 23. TAENIOMA PERPUSILLUM. Photomicrographs by T. T. McCabe.

sion of having arisen in a secund series from the dorsal side of the prostrate axis.

Starting at the third, fourth or fifth segment from the base, the erect secondary axes give rise to determinate branches alternately at an interspace of two to nine segments (fig. 1). These branches, in contrast to the indeterminate axes, are five cells in width, except at the base, and are therefore flat (figs. 1, 2, 11, 12, 14). At an early stage in development, three hairs are formed at the tip of each determinate branch (figs. 1–3, 11–14) whereupon all further growth in length by segment formation ceases in such a branch.

When a developing determinate branch is two or three segments long, it frequently initiates on its adaxial side an indeterminate branch which in a manner similar to the secondary axes forms determinate branches of a higher order (figs. 1, 7; see also Thompson, 43, fig. 3). This process whereby a determinate or an indeterminate branch of one order gives rise to a higher order of branch of the opposite type is repeated over and over.

Method of Branching. When a branch is to be initiated, the apical cell, which ordinarily divides transversely, forming disk-shaped segments, divides by an oblique wall, leaving a segment which on one side is higher than the other (figs. 5, 7). Through enlargement the higher side of this segment forms a protuberance which is cut off. The cell so formed is the initial of a branch (fig. 6). This method of branching has been termed exogenous branching by Falkenberg (14). The original initial retains its rôle as the apical cell of the axis. Both apical cells next divide in the usual transverse fashion, giving rise to two monosiphonous filaments whose segments eventually undergo division. In the case of the erect axes, the branches formed are always alternate and of the determinate type while the prostrate main axis forms alternate and commonly erect, indeterminate branches. As stated above, a determinate branch usually forms an indeterminate branch on its adaxial side (figs. 1, 7). These branches are also exogenous in origin.

Although indicated in Falkenberg's (14) figure 23 on plate 15, and described and figured by Thompson (43, p. 100, fig. 4), the exogenous manner of branching in *Taenioma* has not received recognition commensurate to its importance. This method of branching is of common occurrence in the Rhodomelaceae, Dasyaceae, and Ceramiaceae but in rarely met with in the Delesseriaceae. In other members of this family, the branches are formed in one or more of the following ways: (1) marginal as in *Membranoptera alata* (Kylin, 24, p. 110, fig. 70), (2) from a cortical cell on the midrib as in *Apoglossum ruscifolium* (Kylin, 24, pp. 85–86, fig. 55b), (3) endogenously as in *Claudea* and *Vanvoorstia* (Papenfuss, 35), or (4) entirely adventitiously from cortical cells

as in *Membranoptera alata* (Phillips, 37) and *Claudea multifida* (Papenfuss, 35).

The only other member of the Delesseriaceae which is known to show exogenous branching is *Caloglossa.* Nägeli (32) as long ago as 1855 showed that in *C. Leprieurii* the branches are initiated by segments which are formed as the result of an oblique division of the apical cell of the parent branch (Nägeli, *op. cit.*, p. 71, pl. 8, figs. 9–10). He also pointed out that the axis is monopodial and that the branches are alternate in position. In manner of growth and branching *Caloglossa* thus agrees with *Taenioma.* It should be mentioned, however, that in *Caloglossa* branches also occur on the midrib, but the exact method of their initiation is unknown. In general, Nägeli's work has not been correctly interpreted, since it is usually stated that in *Caloglossa* the lateral branches are marginal in origin.

Structure of Determinate Branches. The determinate branches are formed alternately at an interspace of two to nine segments on the terete, erect, indeterminate branches (fig. 1). The apical cell of the young branch by transverse division forms segments in the manner characteristic of the Delesseriaceae. When a determinate branch is but two or three segments long, its apical cell frequently divides by an oblique wall, cutting off a segment which gives rise to an indeterminate branch on the adaxial side (fig. 7). Following the initiation of this branch, the apical cell by transverse divisions forms from 12 to 20 segments. There are then formed by alternate oblique divisions two segments (fig. 8) which are similar to those which initiate branches. Each of these two segments gives rise to an apical cell (figs. 9, 10). At this stage, the branch apex is thus crowned with three initials. The latter by transverse division give rise to the three monosiphonous hairs which adorn the tip of the mature determinate branch (figs. 10–14, 2–3).

As has been pointed out by Falkenberg (14) and Thompson (43), the hairs terminate all growth in length by cell formation and are responsible for the determinate character of these branches. According to Børgesen (5) and Okamura (33), intercalary divisions occur at the base of a hair, but the writer can find no evidence of this. The cells of the hairs are formed in acropetal succession by division of the apical cell. Those at the base merely fail to elongate as much as the distal ones and give the false impression of having been formed by intercalary divisions.

While the hairs are in course of formation, the part of the determinate branch posterior to them continues its development. This is best described in connection with figures eight and eleven to thirteen.

At the time that the hairs are initiated, the segments immediately below the two hair-forming ones are still undivided (fig. 8).

The division of the segments to form pericentral cells is shown in figure eleven. It will be seen from this figure that the second and third segments below the large triangular cell, representing the segment which initiated the first hair, have each formed a lateral pericentral cell, while in the following three segments both lateral pericentral cells have been formed. In the seventh and subsequent segments down from the triangular cell, both the transverse pericentral cells have been cut off, but only one in each segment is indicated in the figure. At this stage the segments thus consist of a central and four pericentral cells.

Mature determinate branches, in contrast to indeterminate ones, are flat, except for the segments below and the three to five immediately above the place of insertion of the daughter indeterminate branch, which remain cylindrical. This flat form is produced as the result of the formation of two flanking cells by each of the lateral pericentral cells.

The transverse pericentral cells do not divide and the branch consequently remains only three cells in thickness at the midrib. The method of formation of the flanking cells is shown in the lower three segments in figure twelve. It will be seen that the pericentral cells first divide by an oblique wall, more or less transverse to the branch axis, to form a flanking cell toward the branch apex. The next division is also in a vertical plane and cuts off the second flanking cell from the portion of the pericentral cell below the first-formed flanking cell. After the four flanking cells have been cut off, no further divisions occur in the segments of a determinate branch.

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Explanation of the Figures. Plate 24.

Plate 24. Taenioma. Figs. 5–16, *Taenioma perpusillum*. Fig. 5. Oblique division of the apical cell of an indeterminate branch to form a branch-initiating segment. Fig. 6. Division of a branch-initiating segment to form an apical cell, the cell to the right. Fig. 7. An indeterminate axis with two alternate young determinate branches, each of which has initiated an adaxial indeterminate branch, while the apical cell of the axis has divided by an oblique wall in preparation for the formation of a determinate branch to the right (the oldest of the determinate branches, the one to the right, is in an early stage of hair-formation, as seen in a side view of its apex). Figs. 8–10. Early stages in the formation of the three terminal hairs, the central initial representing the original apical cell of the branch. Figs. 11–13. Young determinate branches showing the further development of the hairs and the division of the segments of a branch initial to form a central cell, four pericentral cells, and the two cells which flank each of the lateral pericentral cells. Fig. 14. Optical longitudinal section parallel to the surface of a determinate branch showing early stages in the formation of tetrasporangia (cover cells were present in the two lower segments but are not indicated in the figure). Fig. 15. Optical vertical section through a row of fertile lateral pericentral cells of a tetrasporangia-bearing branch showing the formation of two cover cells by the stalk cell in the two older segments. Fig. 16. Optical longitudinal section parallel to the surface of a determinate branch with mature tetrasporangia. Fig. 17. *Taenioma macrourum*, terminal portion of a young determinate branch with its two apical hairs in the course of development (material from the Bahamas, *Howe 5708*). (Figs. 5–15, 17, × 780. Fig. 16, × 340.)

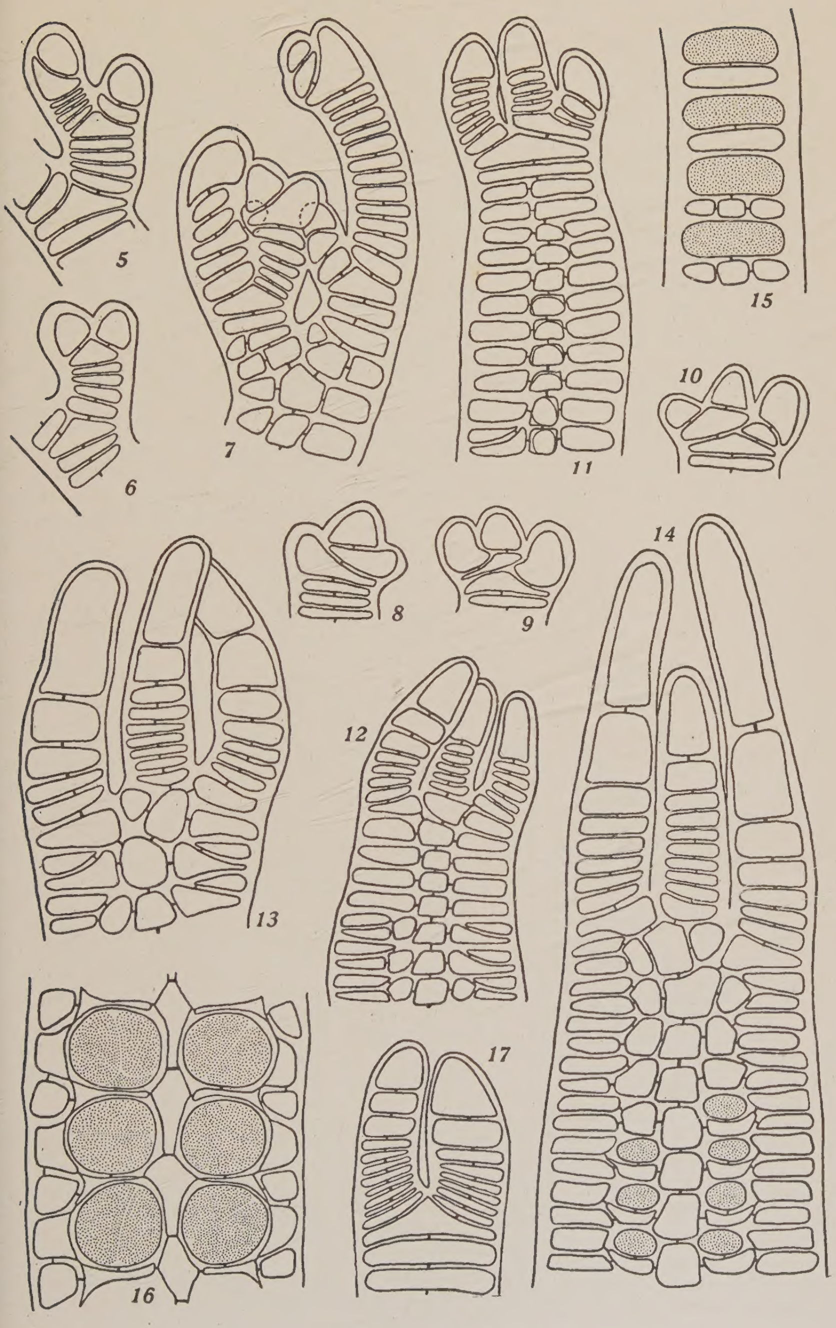


PLATE 24. TAENIOMA.

The division of the two hair-forming segments is similar to that of other segments (figs. 12–14), except that in the distal one, the lateral pericentral cell on the side opposite to the point of attachment of the hair fails to form flanking cells (figs. 2, 14).

No intercalary cell divisions occur anywhere in the thallus of *Taenioma*. Secondary pit connections are formed between neighboring cells, except in the case of the central cells, which do not become secondarily connected to each other nor to other cells.

Although the thallus of *Taenioma* is extremely simple, the construction of the determinate branches is nevertheless in accordance with the plan basic to all Delesseriaceae (cf. Kylin, 24, pp. 67–69, 81–82). Three categories of cells may thus be recognized: (1) a cell-row of the first order, represented by the central cells; (2) a cell-row of the second order, represented by the lateral pericentral cells and the upper of the two flanking cells; and (3) a cell-row of the third order, represented in the determinate branches of *Taenioma* by a single cell, the lower of the two flanking cells (figs. 2, 12–14).

It was stated earlier that *Taenioma* is to be included in the Delesseriaceae rather than in the Rhodomelaceae on the basis of the sequence in which the pericentral cells are formed.

That there is a fundamental difference in the order of formation of the pericentral cells in the Rhodomelaceae and Delesseriaceae was first pointed out by Nägeli (31) in 1847. From his studies of *Hypoglossum Woodwardii,* species of *Polysiphonia* and other representatives of both Delesseriaceae and Rhodomelaceae, Nägeli (29, 30, 31) established that in the Delesseriaceae the two lateral pericentral cells are formed before the two transverse ones (Nägeli, 29, pl. 1, fig. 9). In the Rhodomelaceae, on the other hand, the pericentral cells are formed in a progressive alternate sequence, with reference to the first one, until the circle is completed. The last-formed pericentral cell thus occupies a position diametrically opposite the first-formed (Nägeli, 30, pl. 7, figs. 33–37).

Since the time of Nägeli, hundreds of species of both Delesseriaceae and Rhodomelaceae have been studied by a large number of workers but not a single exception to these plans has been found. In the manner typical of the Delesseriaceae, the two lateral pericentral cells are also the first to be found in *Taenioma* (fig. 11; see also Falkenberg, 14, p. 710, pl. 15, figs. 25–26; and Thompson, 43, p. 101).

In the Delesseriaceae, with the exception of *Taenioma* and *Caloglossa,* lateral organs are not initiated by a segment prior to the formation of its pericentral cells. In the majority of Rhodomelaceae, to the contrary, the lateral organs are initiated before the segment cells have formed pericentral cells. Subsequent to Nägeli, many workers have consequently been concerned with problems relating to the position of the pericentral cells

with reference to the lateral organs and to one another. The following are some of the more important questions which have been studied: (1) the position of the first pericentral cell, (2) whether the second pericentral cell is formed to the left or to the right of the first, (3) whether or not the position of the second pericentral cell is constant in a given species, and (4) whether or not the second pericentral cell follows the spiral described by the lateral organs. For a summary of knowledge concerning these interesting questions, the reader is referred to the excellent paper by Rosenberg (38, pp. 5–9, 31–32).

In this connection, it may be mentioned that in the Dasyaceae, according to Rosenberg (38), the pericentral cells are formed in a progressive left-hand sequence, with reference to the first one, as seen from the outside, so that in the completed circle the youngest lies to the right and next to the first-formed. The Dasyaceae, Delesseriaceae and Rhodomelaceae thus differ very sharply from one another in regard to the plan in which the pericentral cells are formed. In the remaining family of the Ceramiales, the Ceramiaceae, typical pericentral cells are of course not formed.

In addition to the difference in plan of pericentral cell formation, the Delesseriaceae may also be distinguished from the Rhodomelaceae, as was pointed out by Falkenberg (14, p. 713), by the fact that in the Delesseriaceae the lateral pericentral cells always form two flanking cells, which in the majority of forms function as the mother-cells of initials which give rise to lateral rows of cells. Each of these flanking cells has a primary pit-connection with the pericentral cell and their combined length equals that of the pericentral cell.

In the few examples of Rhodomelaceae where a similar formation of flanking cells occurs, only one flanking cell is formed by each pericentral cell. This cell is cut off by a longitudinal division and is therefore as long as the pericentral cell. It may later divide transversely so that there are two (or more ?) flanking cells. Only one of these cells, however, will be united to the parent pericentral cell by a primary cytoplasmic connection.

In regard to the manner of flanking cell formation *Taenioma* thus also shows itself to be a member of the Delesseriaceae.

## Reproduction

Tetrasporangia. Several of the earlier workers have recorded tetrasporangia in *Taenioma*. The development of these organs has, however, been studied only by Thompson (43). The writer's observations are in agreement with those of this author.

The sporangia are cut off in acropetal succession from the lateral pericentral cells in the expanded distal portion of the determinate branches (fig. 14). Each pericentral cell forms only one sporangium. It is separated by a concave wall from the

terminal end of the pericentral cell and is in cytoplasmic communication with this cell only (fig. 14).

After a sporangium has been initiated, the remaining portion of the pericentral cell, at this stage referred to as the stalk cell, divides by two walls parallel to the surfaces, forming a small cover cell on each (fig. 15). In *Taenioma* the cells so formed never enlarge or divide to form a protective layer over the sporangium, but remain as rudimentary cover cells on either surface of the stalk cell. The sporangia thus remain exposed on two sides during their entire existence (figs. 4, 16). In the mature sporangia-bearing branch, the central cells of the branch and the stalk cells of the sporangia are considerably stretched by the enlarging sporangia, and the marginal cells become connected by secondary pit-connections to neighboring marginal and stalk cells (fig. 16).

The method of sporangium-formation in *Taenioma* is comparable to that in *Vanvoorstia* (Papenfuss, 35, figs. 67, 68). In both genera the sporangia are formed by pericentral cells which have not yet become corticated, and the cover cells are formed after the sporangia have been initiated. The subsequent development in the two genera is different, however, in that the primary cover cells grow and divide in *Vanvoorstia,* forming a complete protective tissue over the sporangia, whereas in *Taenioma* the cover cells serve no protective purpose and the sporangia remain exposed.

By the method of sporangium-formation, *Taenioma* thus again shows itself to be a member of the Delesseriaceae. In the Rhodomelaceae, the pericentral cells destined to produce sporangia first form two cover cells by longitudinal divisions and then divide by a transverse wall to form the sporangium (cf. Kylin, 28, p. 173). The situation in the Rhodomelaceae is thus the reverse from that in *Taenioma* and *Vanvoorstia* where the sporangium is the first cell to be cut off by a fertile pericentral cell.

In those Delesserieae and Rhodomelaceae in which the sporangia are initiated by cells other than the pericentral cells this sequence is maintained (cf. Kylin, 28, pp. 170, 174–175). The significance of this distinction between the Delesserieae and Rhodomelaceae will appear later.

Spermatangia and Cystocarps. Sexual organs have been but rarely observed in *Taenioma.* None were present in the writer's material. Spermatangia were recorded for the first time by Schmitz and Hauptfleisch (42, p. 415) in 1897, and for a second time by Thompson (43) in 1910. From the descriptions of these authors and from the figures of Thompson, it is clear that the spermatangia are formed directly on the branches (the determinate branches) as they are in all other Delesseriaceae. In the Rhodomelaceae the spermatangia are usually formed on trichoblasts, although, as pointed out by Falkenberg (14), there are exceptions to this rule. In a few genera such as *Bostrychia* and

*Rhodomela,* the spermatangia are formed on ordinary polysiphonous branches.

According to Thompson, the lateral pericentral cells become divided by vertical walls prior to the formation of spermatangial mother-cells. This statement requires verification. In other monostromatic Delesseriaceae the primary cells become divided by two walls parallel to the surface, forming a layer of cells on each surface. The superficial cells so formed then become divided by vertical walls to form the spermatangial mother cells. The spermatangia are formed on the surface of these cells. The mature spermatangial sorus is thus composed of five cells in thickness. Thompson describes and figures the mature sorus of *Taenioma* as consisting of four cells in thickness.

Cystocarps have been observed with certainty only by Thompson (43). The record by Collins and Hervey (11) of a mature cystocarp in material from Bermuda (Phyc. Bor.-Amer. no. 1935) is very doubtful, since duplicate material of this collection which was examined by Howe (20) proved to be a rhodomelaceous alga. The writer has found the same to be true of the duplicate material in the Herbarium of the University of California.

Nothing is known of the development of the procarp in *Taenioma* and very little concerning the cystocarp. According to Thompson, the cystocarps occur on the terete branches. This may seem unusual in view of the fact that the sporangia and spermatangia occur on the flattened determinate branches. From the position of the cystocarp Thompson concluded that this organ is a modified branch. This assumption is logical. It seems likely, however, that the cystocarps are initiated on young determinate branches but that such branches do not complete their normal growth and in the course of development of the cystocarp become incorporated in its wall. Comparable conditions obtain in *Claudea* and in *Vanvoorstia* (cf. Papenfuss, 35, pp. 26, 43, figs. 23, 42, 43, 51).

From the general shape of the cystocarp and the gross structure of the gonimoblast, Thompson concluded that *Taenioma* belonged in the Rhodomelaceae. Through the researches of Falkenberg and of Kylin and his students, we now know, however, that there are no sharply defined and constant differences between the Rhodomelaceae and Delesseriaceae with respect to the development and structure of the cystocarp.

## Taxonomy

In addition to *T. perpusillum,* which was described by J. Agardh (1, 2) from material collected by Liebmann at St. Augustin on the Pacific coast of Mexico, two other species, *T. macrourum* Thuret (9) and *T. Clevelandii* Farlow (15), have been credited to *Taenioma.*

*Taenioma macrourum* was established by Thuret in 1876 upon material collected by Schousbee at Tangier, Morocco. In considering his plant as distinct from *T. perpusillum,* Thuret seems to have been influenced more by the widely separated stations of the two species than by morphological differences. Without being aware of it, he did, however, describe and figure a feature whereby *T. macrourum* can readily be distinguished from *T. perpusillum* as characterized by J. Agardh. According to Thuret the tetrasporangia-bearing branches of *T. macrourum* terminate in two hairs while those of *T. perpusillum,* according to J. Agardh, end in three hairs. This character is of the first importance in separating these two species as will be shown farther on.

Bornet (8) in 1892 reduced *T. macrourum* to the synonymy of *T. perpusillum,* and this point of view has been accepted by the majority of workers, including De Toni (12), Howe (in Thompson, 43, p. 98, note), Børgesen (5, 6), Okamura (33) and others. Falkenberg (14) and Schiffner (39, 40), on the other hand, have retained *T. macrourum* as an independent species. Schiffner does not give his reasons for so doing but Falkenberg, upon comparing *T. perpusillum* from the Pacific with material of *T. macrourum* from the Mediterranean, concluded that the former species lacked the long monosiphonous terminal hairs characteristic of the latter. The branches in *T. perpusillum* were also separated by an interspace of more segments, causing the plants to be less compact than in *T. macrourum.*

Although it is not possible to uphold the characters relied upon by Falkenberg, the writer's study nevertheless favors separation of the two species. As mentioned earlier the plants at hand of *T. perpusillum* came from Hawaii and South Africa. The observations on *T. macrourum* are based upon material from the Bahamas (*Howe 5708,* as *T. perpusillum*—Herb. Univ. Calif. no. 207218) and from the Adriatic (Schiffner, Alg. mar. no. 860—Herb. Univ. Calif. no. 495029).

From the account of the structure of the determinate branches of *T. perpusillum* it is seen that the terminal hairs are formed in a very precise manner. In this species the apical cell of a developing determinate branch forms a number of disk-shaped segments by transverse divisions and then, by alternate oblique divisions, two segments which on one side are higher than the other. These two segments form initials which together with the original apical cell of the branch give rise to the three terminal hairs characteristic of this species. In *T. macrourum* only one terminal segment is formed by an oblique division of the apical cell of a determinate branch and as a result the tips of these branches are crowned with only two hairs (fig. 17; also see Thuret, 9, pl. 25, fig. 1; Falkenberg, 14, pl. 15, figs. 21, 22; Børgesen, 5, fig. 337).

Since none of the plants studied by the writer showed part of the branches ending in three hairs and the rest in two, there

is reason to believe that the number of hairs is constant in a species: in *T. perpusillum* the determinate branches invariably end in three hairs while in *T. macrourum* they end in two.

Another feature which may be of importance in separating *T. perpusillum* from *T. macrourum* is that in the former the determinate branches usually form an adaxial indeterminate branch near their base, while in the latter such branches are rare. Consequently in *T. perpusillum* the thallus is more profusely branched than in *T. macrourum.* Before it could be conclusively stated, however, that this latter character is of systematic value, it would be necessary to examine more material of *T. macrourum* than has been available to the writer.

Bornet (8) when uniting *T. perpusillum* and *T. macrourum* listed as a synonym the South African species described by Kützing (23) in 1863 as *Polysiphonia nana,* while Falkenberg (14) gave the latter as a synonym of *T. macrourum.* Kützing figured *P. nana* as having some branches ending in a large inflated, apical cell and others ending in two hairs. If *P. nana* were a species of *Taenioma,* it would thus be logical to consider it as representative of *T. macrourum;* and since *nana* is the older specific name it would have priority over *macrourum.* The writer has not had the opportunity of examining Kützing's material nor has he been able to identify with certainty a South African plant with Kützing's species. Judging from Kützing's description and figure, however, there is little reason for believing that *Polysiphonia nana* is representative of the genus *Taenioma.* It seems more likely that the species is a rhodomelaceous alga. The segments show four parallel, vertically elongated, cells of the same length, which suggest pericentral cells as seen in surface view.

The third species of *Taenioma, T. Clevelandii,* was described by Farlow (15) in 1877 from material collected by Cleveland at San Diego, California. In a recent paper Hollenberg (19) records having again found the species; and he also refers to specimens in the Herbarium of the University of California. According to Hollenberg *T. Clevelandii* was reduced to the synonymy of *T. perpusillum* by De Toni (13). The cited work of De Toni, however, contains no statement to this effect.

From a study of the material in the Herbarium of the University of California and from the account of Hollenberg, it is clear that *T. Clevelandii* is not a species of *Taenioma* but belongs to the genus *Platysiphonia* Børgesen (7). Weber-van Bosse (45) already in 1896 remarked upon the great similarity in structure between *T. Clevelandii* and *Sarcomenia miniata,* which is now *Platysiphonia miniata. T. Clevelandii* differs from the other two species of *Taenioma* in the following important features which it shares with *Platysiphonia:* (1) The branches are endogenous in origin. (2) No terete branches are formed, that is, the lateral pericentral cells in all branches divide to form two flanking cells. (3) It does not

have determinate branches which end in hairs. (4) In the tetrasporangia-bearing branches, the sporangia on one surface are covered by a large cell and on the other by a rudimentary cover cell. These branches thus have a dorsiventral organization. In *Taenioma* both cover cells are rudimentary.

In habit *T. Clevelandii* resembles *Platysiphonia intermedia.* The relation of these species to each other can, however, only be established from a detailed comparative study based on preserved material. Pending such a study, it seems best to retain them as distinct entities.

The nomenclature and the geographical distribution of the species of *Taenioma* may be summarized as follows:

Taenioma perpusillum (J. Ag.) J. Agardh, Sp. Alg. 2(3): 1257. 1863. *Polysiphonia perpusilla* J. Agardh, Öfvers. Kgl. Svenska Vetensk.-Akad. Förhandl. 4: 16. 1848.

Geographical distribution. Pacific Ocean: St. Augustin, west coast of Mexico (type locality, J. Agardh, *loc. cit.*); Hawaiian Islands (Chamberlain, 10, p. 33; Papenfuss in the present article); Japan (Okamura, 33, p. 26, in part); Tonga Islands (Grunow, 17, p. 50); Molucca Islands (Heydrich, 18, p. 295). Indian Ocean: Dirk Hartog Island, Western Australia (Askenasy, 3, p. 54); South Africa (Papenfuss in the present article). Atlantic Ocean: Puerto Rico (Thompson, 43, p. 97).

Taenioma macrourum Thuret, in Bornet and Thuret, Notes Algologiques, Fasc. 1: 69. 1876.

Geographical distribution. Mediterranean Sea: Tangier, Morocco (type locality, Thuret, *loc. cit.;* Bornet, 8, p. 297, as *T. perpusillum*); Balearic Islands (probably this species, De Toni, 13, p. 358, as *T. perpusillum*); Naples (Berthold, 4, p. 523; Falkenberg, 14, p. 709); Dalmatia, Adriatic (Schiffner, 39, p. 158—Alg. mar. no. 860!; 40, p. 302). Atlantic Ocean: Canary Islands (Børgesen, 6, p. 143, as *T. perpusillum*). Caribbean: Caracas, Venezuela (Bornet, 8, p. 297, as *T. perpusillum*), Barbados (probably this species, Vickers, 44, p. 62, as *T. perpusillum*), Bahamas (Thompson, 43, p. 97; Howe, 21, p. 564, as *T. perpusillum, Howe 5708* !), Virgin Islands (Børgesen, 5, p. 338, as *T. perpusillum*). Pacific Ocean: Japan (Okamura, 33, p. 26, as *T. perpusillum,* in part).

**Platysiphonia Clevelandii** (Farlow) Papenfuss, comb. nov. *Taenioma Clevelandii* Farlow, Proc. Am. Acad. Arts and Sci. 12: 236. 1877.

Geographical distribution. California: San Diego (type locality, Farlow, *loc. cit.*); San Pedro (Herb. Univ. Calif. no. 96445, *Mrs. H. D. Johnston,* Jan. 27, 1900, with tetrasporangia; no. 315651, *H. P. Johnson,* Dec. 28, 1895); Carmel Bay (Herb.

Univ. Calif. no. 274026, *N. L. Gardner,* May, 1916, with tetrasporangia); near Pacific Grove (Hollenberg, 19, p. 534).

### Discussion

From the preceding account of the structure of the thallus and the development of the tetrasporangia it is clear that Falkenberg (14) was justified in removing *Taenioma* from the Rhodomelaceae and placing it in the Delesseriaceae. Within this family the genus belongs in the sub-family Delesserieae; and from a comparison with other genera, it is apparent that *Taenioma* is the simplest of known Delesserieae. This is shown both by the structure of the thallus and the exposed condition of the sporangia. In the indeterminate branches, the lateral pericentral cells do not function as the mother-cells of lateral initials, while in the determinate branches, where they do act as such, the cell-row of the second order is composed of but two cells and that of the third order is represented by only one cell. As in other Delesserieae, the sporangial mother-cells first form a sporangium and later the cover cells; but in contrast to other members of this sub-family the cover cells in *Taenioma* are of a rudimentary character and at best can only be classed as incipient cover cells. They have no protective value at any stage in the development of the sporangia. These organs consequently always remain exposed on two sides.

In his monograph on the Delesseriaceae, Kylin (25) divided the family into a number of groups. To these was added the *Claudea*-group by Papenfuss (35). *Taenioma* possesses certain of the characters of the latter group but differs from it and all other groups in one very important feature, namely, the exogenous origin of the branches. This method of branch initiation is, however, also shown by *Caloglossa,* which Papenfuss included in the *Claudea*-group. *Caloglossa* was placed in this group on the basis of the structure of the blade and the formation of procarps on only one surface of the blades; and since it has generally been supposed that the branches in *Caloglossa* are marginal in origin, the *Claudea*-group was circumscribed so as to include forms with this method of branching. From the work of Nägeli (32) it is obvious, however, that the branches in *Caloglossa* are exogenous in origin. It thus becomes necessary to remove this genus from the *Claudea*-group, and to amend the group so as to exclude forms showing marginal branching.

Since *Taenioma* and *Caloglossa* differ from all other known Delesseriaceae by the exogenous origin of their branches, it seems likely that these genera will prove to be closely related. This question could be considered more profitably, however, after the development of the procarp and the cystocarp had been studied in both genera. It may be noted that structurally the thallus of *Caloglossa* is more complex than that of *Taenioma.*

A question which may here be considered is whether *Taenioma* exhibits a primarily simple or a reduced condition. Since the structure of the thallus, especially that of the indeterminate branches, is comparable to that of many Rhodomelaceae, the most highly evolved Florideae, it may be argued that the thallus of *Taenioma* has been reduced. None the less, the exposed state of the sporangia, coupled with the simplicity of the thallus, favors the view that *Taenioma* actually represents a primitive condition within the Delesseriaceae, that is, a genus which has retained certain relatively simple features characteristic of Ceramiales lower than the Delesseriaceae and other characters which have become elaborated or which have been eliminated in the higher Delesseriaceae.

Within the Delesserieae the origin of tetrasporangia from pericentral cells probably is a feature which in itself is indicative of a primitive condition. But it is difficult to evaluate this character in *Taenioma* and related genera, since the thallus is very narrow and the only other cells which conceivably could form sporangia would be the flanking cells. In none of the Delesseriaceae, however, do marginal cells form sporangia. In contrast to *Taenioma,* the sporangia in higher Delesserieae are formed by cortical cells and not by pericentral or other primary cells.

In view of the primitive features exhibited by *Taenioma,* it becomes of interest to know whether the genus throws light on the relationships of the Delesseriaceae. Although it is not possible to point to any particular transitional type which could be conceived as forming a link between *Taenioma* and any other family of the Ceramiales, yet certain facts have come to be recognized which have a bearing on the phylogeny of the order and which necessitate a change in the accepted view regarding the relative positions of two of the families, namely, the Delesseriaceae and the Dasyaceae.

In works on the algae, the Dasyaceae are usually placed above the Delesseriaceae. From a review of the literature and the results of the present study it is apparent, however, that the Dasyaceae are phylogenetically lower than the Delesseriaceae. Certain facts furthermore suggest that the Dasyaceae evolved from Ceramiaceae-like ancestors and that the Delesseriaceae and the Rhodomelaceae developed from Dasyaceae-like plants.

It is commonly agreed that the Ceramiaceae include the most primitive Ceramiales. This view is supported by the following facts: (1) The thallus in general is relatively simple, consisting in lower forms of branched monosiphonous filaments but becoming polysiphonous or corticated in higher forms. Typical pericentral cells, that is, cells which from the beginning are as long as the central cells, are, however, not formed. (2) In the majority of forms the sporangia and the gonimoblasts are naked.

(3) The auxiliary cell in lower forms is supplied with a diploid nucleus via an intermediary connecting cell.

Although Kylin (24, 26, 27) has on several occasions expressed the view that the Delesseriaceae and the Rhodomelaceae represent two parallel lines of development, with the Rhodomelaceae occupying a somewhat higher level than the Delesseriaceae, he has, nevertheless, always placed the Dasyaceae above the Delesseriaceae. Phycologists in general have adopted the arrangement of Kylin.

From the work of Rosenberg (38) and others on the Dasyaceae several facts may be cited which indicate that this family is less advanced than the Delesseriaceae and more closely related to the Ceramiaceae than are the Delesseriaceae. The most significant single fact supporting this view is that in the Dasyaceae the auxiliary cell receives a diploid nucleus from the fertilized carpogonium via a connecting cell. This feature is characteristic of the lower Ceramiaceae, but has been lost in the Delesseriaceae. Other primitive features of the Dasyaceae are: (1) The sporelings remain monosiphonous for a long time (Killian, 22) as contrasted with those of the Delesseriaceae and Rhodomelaceae in which pericentral cells are formed at an early stage in development. (2) The pericentral cells are of a rudimentary character in certain genera. (3) The sporangia remain partially exposed.

It may also be added that Falkenberg (14) considered the sympodial method of branching of the Dasyaceac as a character which is primitive in comparison with the monopodial branching characteristic of the Rhodomelaceae. Whether the sympodial habit actually is a primitive feature or whether it is a derived condition which has become established in the Dasyaceae would, however, be difficult to decide. It would seem that in exogenous branching a reversal from the monopodial to the sympodial habit or vice versa is one which would not entail profound change. Furthermore, in the Ceramiaceae, which are more primitive than the Dasyaceae, some forms show monopodial and others sympodial branching (Feldmann-Mazoyer, 16, p. 123).

According to Kylin (28, p. 134) the sporelings of the Dasyaceae show monopodial branching. If this were correct it would indicate that the sympodial habit of the older thallus was acquired in the course of evolution of the family. However, from the observations of Killian (22) on the sporelings of *Dasya arbuscula,* upon which work Kylin's statement is based, it seems evident that sympodial branching is also characteristic of the sporelings of the Dasyaceae, or at least of those of *D. arbuscula.* This is the interpretation which Oltmanns (34, p. 322) also gives of Killian's work.

As to the relative position of the Delesseriaceae and the Rhodomelaceae the available facts favor the conclusions of Kylin (24, 26, 27) that these families represent two parallel lines of

evolution, with the Rhodomelaceae occupying a somewhat higher level than the Delesseriaceae. In support of this view Kylin (26, 27) cites three facts: (1) The Rhodomelaceae are in a more active state of speciation. (2) In the Rhodomelaceae the pericarp is initiated prior to fertilization whereas in the Delesseriaceae it is formed after fertilization. (3) In the Rhodomelaceae, the cover cell of the procarp is a specialized cell which degenerates if fertilization fails to occur while in the Delesseriaceae it is comparable to an ordinary vegetative cell (Kylin, 24, p. 102; 28, p. 286).

It may be pointed out, however, that the two latter distinctions only hold when the Rhodomelaceae are contrasted with the Delesserieae. In the higher Delesseriaceae, that is, in the Nitophylleae, the cover cell of a procarp behaves like that of the Rhodomelaceae (Kylin, 28, p. 286); and in certain members of this sub-family (e.g., *Phycodrys sinuosa* Kylin, 24, figs. 46h, 47d–g; *Acrosorium acrospermum* Papenfuss, 36, fig. 16) the pericarp is initiated prior to fertilization.

To the points cited by Kylin may now be added a fourth which lends support to the view that the Rhodomelaceae are phylogenetically higher than the Delesseriaceae. In the Rhodomelaceae the sporangial mother-cells cut off the cover cells before the sporangia are initiated whereas in the Delesserieae the cover cells are formed after a sporangium has been initiated. In the latter group the young sporangia are thus exposed while in the Rhodomelaceae they are protected. In *Taenioma,* the most primitive of known Delesseriaceae, the cover cells are rudimentary and serve no protective purpose at any stage in the development of the sporangia, while in the related *Platysiphonia* the cover cells are well developed on one surface of the fertile branches and rudimentary on the other. Thus *Platysiphonia* may be said to form a link between *Taenioma* and *Vanvoorstia* in which latter genus the cover cells are well developed on both surfaces of the fertile blades (Papenfuss, 35).

As to the probable ancestors of the Delesseriaceae, there is reason to believe that they may have evolved as an off-shoot from the stock which gave rise to present-day Dasyaceae. Three facts especially may be cited in support of this view: (1) In the Delesserieae as in the Dasyaceae the sporangial mother-cells first form a sporangium and then the cover cells. (2) In both the Delesserieae and the Dasyaceae the cover cell of the procarp is comparable to a vegetative cell and functions as such if fertilization fails to occur. (3) In the Delesseriaceae in general, but more particularly in the Delesserieae, as well as in the Dasyaceae the pericarp is not initiated until after fertilization.

It is of interest to note that in these three features the Rhodomelaceae have advanced beyond both the Dasyaceae and the Delesseriaceae. It may be mentioned, however, that the higher

Delesseriaceae, for example, certain members of the Nitophylleae, not only share some of these advances with the Rhodomelaceae but have attained a degree of simplicity which surpasses that shown by any of the Rhodomelaceae. It is thus found that: (1) In the Nitophylleae growth of the mature thallus is usually marginal whereas in the Rhodomelaceae it is primarily apical. (2) In the Nitophylleae intercalary cell divisions are of common occurrence while such divisions, to the writer's knowledge, are unknown in the Rhodomelaceae. (3) In the Nitophylleae the reproductive organs are formed in parts away from the central axis of the thallus whereas in the Rhodomelaceae they generally are localized on the axis, that is, the pericentral cells. It is of interest to note that an advance in the same direction is shown by some of the higher Rhodomelaceae, such as *Laurencia* and *Ricardia.* In these genera the sporangia are no longer formed by pericentral cells but by cells farther away from the central cells (cf. Kylin, 26, p. 101).

Finally, in regard to the probable prototypes of the Rhodomelaceae, it seems likely that this family also may have evolved from Dasyaceae-like algae, although at a time subsequent to the separation of the Delesseriaceae. It is well known that the Rhodomelaceae have a number of characters in common with the Dasyaceae. The similarity in the habit of the thalli, the formation of the sporangia from pericentral cells, and the corresponding position of the spermatangia are some of the more important points of agreement which may be mentioned. It is of interest to note in this connection that in *Heterosiphonia coccinea* (Dasyaceae) the pericentral cells are formed in the manner characteristic of the Rhodomelaceae except in the fertile segments of female plants where they are formed in typical dasyacean fashion (Rosenberg, 38). In this particular species the sporangia and their cover cells are also formed in the sequence characteristic of the Rhodomelaceae. This member of the Dasyaceae thus shows certain morphological features which have become established in present-day Rhodomelaceae. It may further be mentioned that Falkenberg (14) considered the Dasyaceae, as now recognized, as a sub-family in the Rhodomelaceae and regarded them as the ancestors of all other Rhodomelaceae.

A schematic representation of the probable interrelationships and lines of development of the families of the Ceramiales is given in text figure 1.

## Summary

The results of this study show that *Taenioma* does not belong to the Rhodomelaceae, in which it has been placed by certain writers, but to the Delesseriaceae. This is shown by the plan of pericentral cell formation, the manner of division of the lateral

pericentral cells, and the method by which the sporangia are formed.

From the simple structure of the thallus and the exposed condition of the sporangia, it is concluded moreover that *Taenioma* is the simplest of known genera of the Delesseriaceae.

The branches of *Taenioma* are exogenous in origin. Although characteristic of the other families of the Ceramiales, this method of branching is rarely encountered in the Delesseriaceae and in addition to *Taenioma* is known to occur in *Caloglossa* only.

The sporangia are initiated by the lateral pericentral cells and are formed before the mother-cells have cut off cover cells. The latter feature is recognized as one whereby the Delesseriaceae

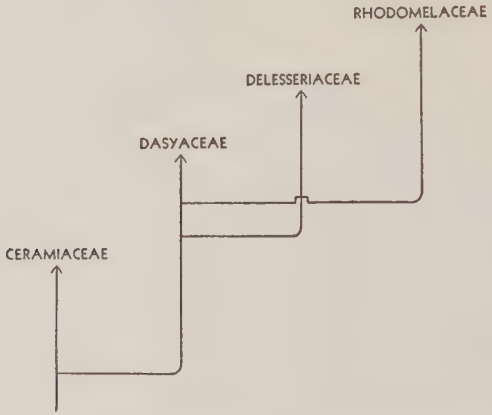


Fig. 1. Diagrammatic representation of the probable interrelationships of the families of the Ceramiales.

may be distinguished from the Rhodomelaceae. In the Rhodomelaceae the mother-cells first form cover cells and then a sporangium.

*Taenioma perpusillum* and *T. macrourum* are considered as separate species. The primary distinguishing feature lies in the fact that the determinate branches of the former form three and those of the latter two terminal hairs. These hairs are initiated in a precise manner by the apical cell and do not vary in number.

*Taenioma Clevelandii,* the only other species which has been credited to *Taenioma,* is transferred to the genus *Platysiphonia* with which it is shown to share various morphological features.

The phylogeny of the Ceramiales is discussed. Evidence is produced to show that the Delesseriaceae are more highly evolved than the Dasyaceae. Additional evidence is furnished in support of the view of Kylin that the Rhodomelaceae are the most highly evolved Ceramiales. It is concluded that the Dasyaceae evolved

from Ceramiaceae-like and the Delesseriaceae and Rhodomelaceae from Dasyaceae-like ancestors.

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After the study had been completed, it was learned from Dr. C. K. Tseng that he had also been working on *Taenioma,* and had arrived at the same conclusions as the writer with respect to the systematic position of the genus and the taxonomy of the species.

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# NOTES ON THE ALGAL GENUS TAENIOMA[1]

C. K. Tseng

The algal genus *Taenioma* (Delesseriaceae, Rhodophyceae) was founded by J. G. Agardh (2, p. 1256) on *Polysiphonia perpusilla* which he (1, p. 16) himself previously had described from material collected by Liebmann at St. Augustin on the Pacific coast of Mexico. The then monotypic genus was characterized by (1) a filiform, dichotomously branched frond with polysiphonous, articulate, noncorticate filaments; (2) the presence of marginal cells half the length of the segments on the flattened portion of the frond; and (3) dilated, vittiform stichidia bearing tetrasporangia (then known as sphaerospores) in a double series. The genus was placed by its author, together with *Sarcomenia,* in the tribe Sarcomeniae which was then placed in the family Rhodomelaceae but later more properly removed by Schmitz (19) to the Delesseriaceae.

Thuret (7, p. 69, pl. 25) added another species to the genus, namely *Taenioma macrourum,* citing as a synonym *Hutchinsia macroura* Schousboe in herb. The type material came from Tangier, Morocco, in the Mediterranean. Not having seen J. Agardh's specimen of *T. perpusillum* Thuret, in describing his species, expressed some doubt as to the specific difference between the Mediterranean form and the one from the Pacific. In keeping the two separate, he was probably influenced by the widely separated regions from which the two plants were collected, some apparent differences in size and color, and especially the presence in the Mediterranean plant of two apical hairs which were presumably absent in the alga from the Pacific. It should be noted, however, that J. Agardh, *op. cit.,* did mention the presence of apical hairs in his plant: "Stichidium . . . apice saepe in fila minuta 3 . . . excurrens." Examination of Agardh's type specimen by Howe (*in* Thompson, 21, p. 98) has confirmed this. The writer has also examined a fragment of the original specimen deposited in the herbarium of the New York Botanical Garden and is in perfect agreement with Howe.

Several years after the publication of *Taenioma macrourum* Thuret, Bornet (6, p. 297) examined a specimen of *T. perpusillum* J. Ag. and came to the conclusion that the Pacific and the Mediterranean plants are not separable specifically. Later, Heydrich (12, p. 295) and De-Toni (9, p. 732) adopted Bornet's view. Schmitz and Hauptfleisch (20, p. 415), however, retained both species. In his classical work on the Rhodomelaceae, Falkenberg (10, p. 709, pl. 15, fig. 21–29), devoted some space to the morphology of the Mediterranean plant, which he separated from the Pacific alga chiefly on the basis of its having long monosiphonous

[1] Contribution from the Scripps Institution of Oceanography, New Series, No. 230.

apical filaments on the flattened "leaves," presumably absent in *T. perpusillum* J. Agardh. This, as already pointed out above, is not correct. Falkenberg also mentioned that the two species differed in the nature of the branches. He remarked that in the Mediterranean plant the cylindrical segments of the side branches and also those of the axis between two branches were so short and compact that it was easily distinguishable from the Pacific plant, which was much slenderer and more loosely branched. While it is true that the Pacific alga has much longer side branches, the shortness and compactness of the segments are similar in both cases. It is no wonder, therefore, that later authors (cf. Collins and Hervey, 8, p. 117; Børgesen, 4, p. 341; and Okamura, 17, p. 26) in trying to differentiate the two species on this basis, could not see the desirability of keeping them apart.

Thompson (21) published a detailed study of the morphology of *Taenioma,* using two different sets of materials collected by Howe at Porto Rico (Puerto Rico) and at West Caicos in the Bahamas. She was probably the first to note some of the important differences between *T. perpusillum* and *T. macrourum* although she discussed both forms under the latter name. Such differences between these two collections as the branching and the number of apical hairs and segments in the flattened shoots have been correctly emphasized. In an editorial note in Thompson's paper, Howe justified that author's identification of the Bahamian plant with the Mediterranean species. He questioned, however, "the identity of this *T. macrourum* with the previously described *Taenioma perpusillum* of J. Agardh . . . ," remarked that his Puerto Rican plant and the type of J. Agardh's species from Mexico are "essentially the same except that the terminal hairs are much longer and more luxuriant in the Porto Rican plant," and concluded that he was "inclined to agree with Bornet . . . with Heydrich . . . and with De-Toni . . . in considering *Taenioma macrourum* (Schousb.) Thur. a synonym of *Taenioma perpusillum* J. Ag."

Howe seemed to have regarded the differences of these two sets of specimens, which he considered to belong to the same species, as a matter of ecological influence. He made the remark that the Bahamian plants "were found growing in an inland pond or lake, having evidently a subterranean communication with the sea—a place where several marine algae of recognizable species were more or less abnormal and peculiar," and the Puerto Rican plants "were growing where they were well exposed to the surge of the open sea." It should be noted, however, that Børgesen (4, p. 341), whose plant was evidently of the same species as Howe's from the Bahamas, found it "in an open place upon reefs of calcareous algae, etc."

To date, phycologists seem to have regarded this problem of the *Taenioma perpusillum-macrourum* complex as satisfactorily

settled, have generally adopted the view of Bornet and his followers, and have conventionally put *T. macrourum* as a synonym of *T. perpusillum* whenever that species is reported.

The third species of *Taenioma* was described by Farlow (11, p. 236) on material from San Diego, California, and was named *Taenioma Clevelandii.* As described, it "has scattered stichidia, is four inches high, and has a striking resemblance to *Griffithsia tenuis* Harv.," and its "stichidial branches terminate in a more or less acute apex instead of two hairs." It was also mentioned that "in the lower part of the frond, the angles between the primary cells are filled with a small but irregular number of secondary cells." All these peculiarities are certainly very different from the characteristics of the *Taenioma perpusillum-macrourum* complex and the writer has long doubted its being a member of this group. He has studied some specimens collected at Moss Beach, Pacific Grove, California (*Hollenberg 3228*) and is fully convinced that it should be separated from *Taenioma.*

Recently Hollenberg (13, p. 534) has pointed out several additional differences between *Taenioma Clevelandii* Farl. and *T. perpusillum* J. Ag., although he still preferred to keep the Californian plant in the same genus. Dr. Papenfuss who has made a critical study of *Taenioma Clevelandii* has agreed with the writer that it does not properly belong to *Taenioma.* He has further decided that it should be transferred to the genus *Platysiphonia* Børg., because (1) its branches are endogenous in origin; (2) it does not form terete branches; (3) it does not have determinate branches ending in hairs; and (4) its tetrasporangial branches have a dorsiventral organization, since the stalk cell of a tetrasporangium forms a large cover cell on one surface and a rudimentary one on the other. These characteristics are so fundamentally different from those of *Taenioma,* that there should no longer be doubt among phycologists that the plant from San Diego should be removed from the genus *Taenioma.*

Some years ago, the writer gathered from Hong Kong a collection of a *Taenioma* rich in tetrasporangia. At first, he was inclined to follow others and consider *T. macrourum* Thur. a synonym of *T. perpusillum* J. Ag. The more the specimens and literature were studied, however, the more hesitant he was to do so. After a thorough study of his collection, which has been preserved in excellent condition for microscopic examination, and the extensive collections of Howe, including some fragments of the type specimen of *T. perpusillum* J. Ag., deposited in the Herbarium of the New York Botanical Garden, the conclusion was finally arrived at, that the differences, especially those reported by Thompson and Howe, do exist, and are very constant. Other differences have also been found. The fact that the same form has been reported to occur in sheltered and exposed places and both forms in more or less similar situations naturally eliminates

the possibility of their being ecological forms, at least, so far as the factor of the relative exposure to surf is concerned. Furthermore, the geographical distribution of *T. perpusillum* and *T. macrourum* gives evidence of their distinctness. When fundamental differences between these two forms are constant and without intermediates, and when these cannot be traced to ecological or geographical influences, then there is no alternative than to accept the two forms as separate, independent species.

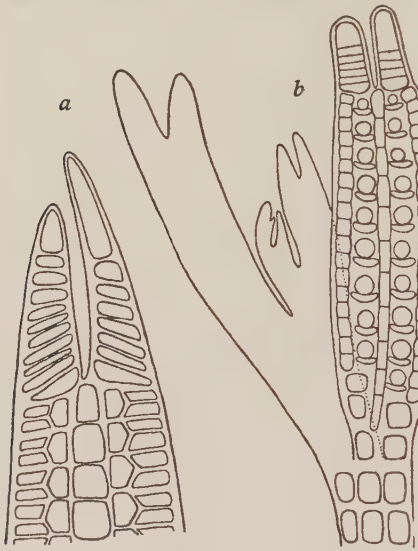

Fig. 1. *Taenioma macrourum* Thuret: *a*, apex of a branchlet showing the two apical hairs, × 560; *b*, upper part of a branch showing a stichidium, × 190.

The most important difference between the two lies in the number of apical hairs. The Puerto Rican and Hong Kong specimens always have three apical hairs on the flattened branchlets and are referable to *T. perpusillum* J. Ag. There are many determinate branchlets which at a glance seem to have only two hairs. A careful study, however, reveals the fact that the oldest hair in the group of three has already dropped off, and the two younger ones are left behind (pl. 25, fig. 5). The Bahamian, Bermudian, and Mediterranean specimens as well as the Japanese plants described and illustrated by Okamura (17, p. 26, pl. 244, fig. 17–19, pl. 245, fig. 5–9, on the contrary, have only two hairs and undoubtedly belong to *T. macrourum* (text fig. 1a). To be sure, Okamura (17, p. 27, pl. 265, fig. 8) mentioned and figured a branchlet with three apical hairs. Whether this was an abnormal form of the normally two-haired plant, or whether Okamura had both species, can be settled only by examination of his specimens which had come from at least two different sources.

The presence of two or of three such apical hairs is neither accidental nor irregular. It is rather a matter of fundamental difference traceable to the behavior of the apical cells of the determinate branchlets. In *T. macrourum*, the apical cell, after having formed the more or less definite number of segments, gives rise by an oblique division to a hair-initiating cell. Later, the apical cell itself assumes the role of hair formation, thus resulting in two hairs (text fig. 1a). In the case of *T. perpusillum*, the apical cell by alternate oblique divisions forms two hair-initials.

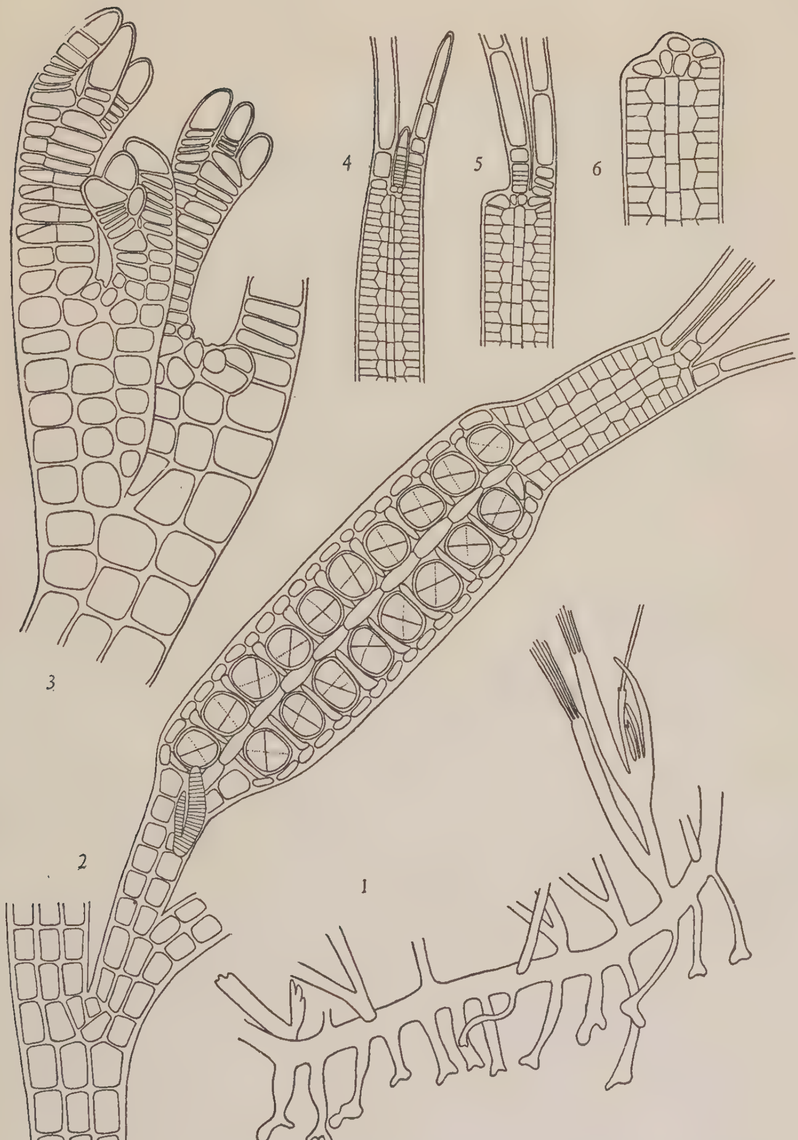


PLATE 25. TAENIOMA PERPUSILLUM (J. Agardh) J. Agardh. FIG. 1. Habit sketch of a portion of a young plant, ×32. FIG. 2. A part of an erect branch, showing a stichidium with tetrasporangia, the differentiation of fertile and sterile portions, and the apical hairs, ×155. FIG. 3. Apical part of a branch showing the apical cells, ×452. FIG. 4. A young branchlet with three hairs in different stages of development, ×155. FIG. 5. An older branchlet with one hair dropped off and two remaining, ×155. FIG. 6. An old branchlet with all three hairs dropped off, leaving three basal cells of the hairs behind, ×155.

One of these develops faster than the other, resulting in two hairs of unequal length. Later the apical cell also gives rise to a hair, resulting in the three terminal hairs characteristic of this species (pl. 25, figs. 2, 3 and 4). In the younger branchlets, while all three hairs are found, the central one generally remains shortest (pl. 25, fig. 4). In older branchlets, the first-formed lateral hair may have dropped off, leaving its basal cell in the original position, while the two which develop later, remain (pl. 25, fig. 5). Then, the other lateral hair and at last the central one drops off, leaving the three basal cells of the original hairs behind. The branchlet at this stage appears stunted, blunt and hairless at the apex (pl. 25, fig. 6). This explains why sometimes there appear to be only one or two hairs, or even hairless forms, instead of the three hairs as described.

Another important difference, already pointed out by Thompson, *op. cit.*, lies in the respective number of segments in the flattened determinate branchlets of these two species. In *T. perpusillum,* there are generally 20 to 35 segments, occasionally as few as 15, and the length of the mature branchlets varies from 0.6 to 1.0 mm. In *T. macrourum,* there are many fewer segments, generally 8 to 20 only, rarely more, and the branchlets are correspondingly shorter, being about 0.25 to 0.40 mm. long when fully mature. In dealing with the length of the branchlets, it is to be noted, the hairs are not included.

There are also observed some differences in the stichidia. In *T. perpusillum,* the stichidium has a cylindrical stalk of 3 to 5 segments followed by the broadened, fertile portion of the "blade" composed of varying numbers of 8 to 14 segments (sometimes as few as 4 and sometimes as many as 17) and then a narrower, sterile portion of 6 to 12 segments upon which are the monosiphonous hairs. Sometimes there are also a few sterile segments between the stalk and the fertile segments (pl. 25, fig. 2). In *T. macrourum,* the cylindrical stalk, with only one or two segments, is followed by the broadened, fertile "blade" and then terminates in the hairs, without an intervening sterile portion as in *T. perpusillum* (see text fig. 1b). This difference between the two species is found in the materials examined. However, in a recent communication Dr. Papenfuss remarks that in his material of *T. perpusillum* the tetrasporangia very frequently extend distally up to the hair-forming segments.

The two species, as they are now separated by the writer, also differ from each other in habit. Generally speaking, *T. perpusillum* is more closely and conspicuously fasciculate, the branching often fastigiate and the branchlets usually alternately disposed, whereas in *T. macrourum,* the branchlets are more loosely disposed and usually secund. In the former species, the erect branches are much taller, about 2 to 3 or more millimeters high, and have as many as twelve determinate branchlets. The latter species has

the erect branches about 1 mm. or less high, with generally 4 to 5 determinate branchlets each.

The original description of the genus by Agardh and the subsequent descriptions of others such as Schmitz and Hauptfleisch are far from complete. Many of the important facts about this group of plants, especially with regard to the sexual organs, were discovered much later. It is Thompson (21) to whom we must turn for our present knowledge of the development of the male organs and the general characteristics of the cystocarps; unfortunately there is no detailed account of the developmental phases of these structures. Collins and Hervey (8, p. 117) mentioned that they found a cystocarp which was, however, lost before a drawing and a description could be made.

By bringing together the collections studied by previous authors and studying these in connection with our own, the following revised description of the genus is made possible.

Taenioma J. Agardh (1863). Plants dorsi-ventral, with horizontally creeping, cylindrical, segmented, polysiphonous, ecorticate, main filaments rhizomatous, giving rise to stout, unicellular rhizoids below and erect branches above. Erect branches arising at rather regular intervals, secundly or alternately, pseudodichotomously branched. Determinate branchlets with short, cylindrical, polysiphonous segmented stalks and flattened, segmented, distal portions. The flattened portion with a distinct midrib of a central siphon surrounded by four pericentral siphons. The dorsal and ventral pericentral cells smaller and the lateral ones larger, each giving rise to two marginal cells, which are very regularly, transversely arranged at the periphery. Apical parts of the determinate branchlets provided with colorless, monosiphonous filaments (hairs). Apical cells large, dome-shaped, dividing by transverse walls. Growth monopodial. Branching exogenous. Tetrasporangia originating from lateral pericentral cells, with two rudimentary cover cells, tetrahedrally divided, in two rows, one on each side of the midrib of the fertile branchlets. Spermatangial branchlets flattened, similar to the tetrasporic ones, fertile portions broadened, spermatangia developed upon cells between axial and marginal cells. Cystocarps urceolate with a terminal ostiole, developed from modified branches.

The general habit of members of this genus is like that of *Herposiphonia* of the Rhodomelaceae, with a horizontally creeping filament giving rise to erect branches at rather regular intervals. The division of the apical cells and the mode of growth are similar to the genus *Caloglossa*. The apical cell repeatedly cuts off disc-like cells below until a more or less definite number is reached and then divides by an oblique wall into two unequal parts (pl. 25, fig. 3). The upper part continues as the apical cell of the filament while the lower, dividing by an oblique transverse wall perpendicular to the first, gives rise to another dome-shaped

cell which becomes the apical cell of the new lateral branch. It follows that the branching is strictly lateral, rather than dichotomous as claimed by J. Agardh, although it may appear subdichotomous. Each segment consists at first of a single disc-like cell, which soon gives rise to two cells on the right and left by two longitudinal divisions, thus forming three cells of similar shape and size in the same plane. Then, two other longitudinal divisions occur, parallel to each other, but perpendicular to the first divisions, thus giving rise to two more cells, one dorsally and one ventrally. The segment thus formed is similar to a typical *Polysiphonia* in having a central cell surrounded by four pericentral cells. The segments of the main filaments, the axis of the branches and the stalks of the determinate branchlets always remain this way. In the distal part of the determinate branchlet, however, the two lateral cells each again undergoes two divisions: first an oblique wall cutting off a triangular cell in the upper part and then a second division cuts off a similar cell in the lower part, thus forming two marginal cells of exactly half the height of the pericentral cells.

In the formation of the tetraspores, each of the lateral pericentral cells undergoes a transverse division, the upper cell becoming the sporangium and the lower one the stalk cell. The sporangium enlarges greatly, still always retaining protoplasmic connection with the stalk cell, and, dividing thrice: a longitudinal division parallel to the flat surface, a transverse one and a third perpendicular to both divisions, give rise to a tetrahedrally divided sporangium (pl. 25, fig. 2). The stalk cells eventually form two cover cells on both surfaces.

Falkenberg (10) mentioned and figured what he suspected to be "antheridia." These are now known to be malformations. Schmitz and Hauptfleisch (20) were the first to correctly mention the spermatia as occurring between the midrib and the marginal cells. Their development was reported by Thompson (21) and the writer's investigations substantiate her conclusions. Briefly, the marginal cells are the first to divide longitudinally; the outer ones remain as such while the inner become the spermatangial clusters by repeated divisions. Later, the pericentral cells on both sides of the axial cells also become involved. Thus, in the fertile portion, all of the cells between the marginal cells and the axial ones give rise to spermatangia. Either the entire "blade" or a part of it becomes fertile. The stalk and the apical hairs remain sterile.

Cystocarps, so far, have been described only by Thompson, *op. cit.* The writer has found, in the Bermuda material, a single urceolate, ostiolate cystocarp with rather broad base and conspicuous neck. Being among crowded filaments in a permanent mount, it cannot be studied in detail. According to Thompson, the characteristics of the cystocarps are those of the Rhodomela-

ceae into which family she preferred to place the genus. It seems that further investigations with better materials are necessary in order to solve this problem. But since the vegetative characteristics as well as those of the tetrasporangia and spermatangia show much closer relationships with such plants as *Sarcomenia* and *Caloglossa,* the writer is inclined to follow Falkenberg, Schmitz, and others in placing this genus in the family Delesseriaceae. Papenfuss (MSS) has arrived at this same conclusion as to the taxonomic position of the genus.

As mentioned above, the genus with its two species is reported from various tropical and subtropical regions, although such records are rather meagre. It seems likely that its distribution is very extensive in warmer waters. The two species can readily be distinguished from each other by sterile characters alone:

A. Plants to 2–3 mm. high, flattened determinate branchlets with 15 to 30 segments, apical hairs three .... 1. *T. perpusillum*

AA. Plants less than 1 mm. high, flattened determinate branchlets with 8 to 20 segments, apical hairs two .......................................... 2. *T. macrourum*

1. TAENIOMA PERPUSILLUM (J. Agardh) J. Agardh, Sp. Alg. 2(3): 1257. 1863. *Polysiphonia perpusilla* J. Agardh, Öfvers. Kgl. Svenska Vetensk.-Akad. Förhandl. 4: 16, 1848. *Taenioma macrourum* Thompson *non* Thuret, Bull. Torrey Bot. Club 37: 97, pl. 9, f. 12, pl. 10. 1910. (In part.)

In a note deposited in the herbarium of the New York Botanical Garden, Howe remarked that the type of this species was mostly sterile, differing considerably in habit from his tetrasporic collection (no. *2433*), but a tetrasporic plant in the type collection was similar. The principal material upon which Thompson based her morphological study of the genus (*Howe 2433*) was growing on a stick of wood collected near low-water mark, at Point Borinquen near Aquadilla, Puerto Rico on June 15, 1903. This material is rich in tetrasporic and spermatangial branchlets; occasionally what seem to be young cystocarps may also be observed.

The Hong Kong materials (*Tseng 2857*) were found tufted on an exposed, surf-beaten rock, together with various small algae, such as *Herposiphonia caespitosa* Tseng, *Gelidium pusillum* (Stackh.) Le Jol., in the lower littoral region at Shek-O, Hong Kong I., on July 4, 1940. They are all tetrasporic. The primary filament is about 90 to 110 μ in diameter, with the segments shorter than the breadth, about 60 to 75 μ long. It sends down vigorous, stout unicellular rhizoids, to as much as 75 μ in diameter, separated from the mother pericentral cells by transverse walls, and more or less expanded at the ends (pl. 25, fig. 1). Erect branches arise from the decumbent filament quite regularly at intervals of 5 to 9 segments. Their axes are cylindrical and segmented like the main filament, giving rise to minor branches or branchlets alternately and fastigiately. The determinate branchlets with cylindrical

stalks below and flattened "blades" above, terminate in three long monosiphonous hairs. The stalks are cylindrical and composed of 3 to 4 segments, about 45 μ in diameter. The blades have conspicuous midribs, to about 70 μ broad when sterile and 0.6 to 1.0 mm. long, generally with 20 to 30 segments. The hairs are about 20 μ in diameter below. The stichidia are very much broadened in their fertile portions, to about 110 μ broad, otherwise like the ordinary branchlets. The tetrahedrally divided tetrasporangia are disposed in two rows along the axis, generally 8 to 14, although fewer or more have been observed. They are about 50 μ in diameter when mature (pl. 25, fig. 2).

A specimen collected by Grunow without giving the date or locality, and another from Tongatabu (Friendly Is.) by Dr. Graeffe all belong here. Heydrich (12) reported that his specimen from Batjan I., North Molucca, had two or three hairs on the stichidia. Most probably, he had this species before him. Askenasy (3) records *T. perpusillum* from Western Australia and Reinbold (18) records it from Sumatra, both without description. In view of the wide occurrence of this species in the Pacific, these identifications are probably correct.

This species, as herein limited, is known from the following regions: St. Augustin, Pacific coast of Mexico (type locality); Fiji and Friendly Is.; Western Australia; Molucca Is.; Sumatra; Hong Kong, China; and Puerto Rico, West Indies.

2. Taenioma macrourum Thuret, in Bornet and Thuret, Not. Alg. 1: 69, pl. 25. 1876. (In part.) *Polysiphonia nana* Kützing, Tab. Phyc. 13: 10, pl. 29, fig. e–f. 1863. *Taenioma perpusillum,* as interpreted by Bornet (6), De Toni (9), Collins and Hervey (8), Børgesen (4), Howe (15), Okamura (17), *non* Agardh.

Since Miss Thompson (21) based her conclusions to a considerable extent upon material collected at West Caicos in the Bahamas (*Howe 5708*) it is of interest to consider the character of these specimens in some detail. The material is tetrasporic with the main filaments generally 60 to 75 μ in diameter and with segments as long as broad. The rhizoids are about 30 μ in diameter. Erect branches are short, less than 1 mm. high, arising in intervals of 4 to 6 segments. They are more loosely and secundly branched than those of the above species. The determinate branchlets have short cylindrical stalks of 1 or 2 segments and "blades" about 60 to 75 μ broad and 240 to 400 μ long (excluding hairs), with 8 to 15 segments and terminating in two colorless, monosiphonous hairs about 25 to 30 μ in diameter at the base. The stichidia are quite young, about 80 to 90 μ broad, with short stalks of 1 to 2 segments, and "blades" having all segments fertile and terminating in two hairs like the vegetative ones.

Another specimen (*Hervey 7433*), collected from South Shore, Bermuda, on February 3, 1913, has vegetative characteristics

similar to the above. There is found, among crowded filaments on a semipermanent mount, a cystocarp which is broadly urceolate, about 360 μ broad and 480 μ long, including a neck about 120 μ long. There is another Bermudian specimen (*Phyc. Bor.-Am. no. 1935*), collected by Hervey, "forming a gelatinous mass with other algae, Bigget Island, April 1913." This, according to Howe (14, p. 518) "shows a small Rhodomelaceous plant bearing some slight resemblance to the *Taenioma*." The writer, however, has found a few fragments of the determinate branchlets of *T. macrourum* Thur. sparsely scattered among a large mass of a blue-green alga and the Rhodomelaceous plant Howe mentioned. They are sterile.

*Taenioma macrourum* has been recorded from the following regions: Tangier, Morocco (type locality) and Naples in the Mediterranean; Canary Is.; Bermuda and West Indies; Japan; ? Cape of Good Hope.

## Summary

A general historical, morphological, taxonomic and distributional survey of the delesseriaceous genus *Taenioma* J. Agardh is given. *T. perpusillum* (J. Agardh) J. Agardh, described from the Pacific coast of Mexico, and *T. macrourum* Thuret, from the Mediterranean, have been regarded, in the past, as belonging to the same species. The conclusion is reached that they represent two distinct species. Important differences are found in the number of apical colorless monosiphonous hairs, the number of segments in the determinate leaf-like branchlets, the stichidia, and the habit and branching of the erect branches. Geographically, both species seem to be widely distributed and are represented, at least in one instance, in the same region (West Indies). A new locality for *T. perpusillum,* namely, Hong Kong on the China coast, is reported.

The writer wishes to express his thanks to Dr. Fred J. Seaver, Head Curator of Herbarium, New York Botanical Garden, for placing the entire collection of *Taenioma* at his disposal, and to Dr. George F. Papenfuss and Dr. Herbert L. Mason of the Department of Botany, University of California, for a critical reading of the manuscript and for making valuable suggestions. The major part of this study was made during the tenure of a fellowship in the Horace H. Rackham School of Graduate Studies, University of Michigan.

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University of California, La Jolla,
March, 1944.

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## REVIEWS

*Marine Algae of the Monterey Peninsula.* By Gilbert M. Smith. Stanford University Press. vii + 622 pages, 98 plates. 1944. $6.00.

The appearance of a flora in a field in which there are less than half a dozen modern treatises is an event of first importance. Professor Smith has filled one of the outstanding gaps in our knowledge of marine phycology. Since the Monterey flora includes 80 per cent of the known seaweeds of the Pacific Coast of the United States, the importance of the book is much greater than the title suggests. Furthermore this locality is of especial historic interest as the type locality of approximately a quarter of the species described from this coast.

That the northeastern Pacific possesses a rich, varied and in some ways unique seaweed flora has been known for a long time. Setchell and Gardner have given excellent accounts of the Cyano-

phyceae, Chlorophyceae and Phaeophyceae but they did not live to complete their work on the red algae. Therefore the present section on the Rhodophyceae as the first comprehensive account, represents a most notable and definite contribution to organized algological knowledge, especially since the red algae constitute between 40 and 50 per cent of the total number of species of green, brown, and red algae occurring along the west coast of the United States.

In the introduction a brief historical sketch is given of seaweed collecting in the Monterey area, from the time of Menzies' visit during 1792–93 up to the death of Gardner in 1937. The annotated list of old and new place names will prove invaluable to future collectors in view of the fact that in a given region so many species appear year after year only along a certain stretch of shore or even on a particular rock. Other topics which are briefly discussed in the introduction include the Monterey and Pacific Coast distribution of algae in relation to ecologic factors, and instructions in seaweed collecting.

In a field which has become as technical as phycology, the adoption of a uniform terminology goes far toward a simplification of the subject matter. The skill with which this has been accomplished would be hard to improve upon. In pursuit of such uniformity the author has, however, borrowed a few terms whose adoption for the algae is open to criticism. Thus for example he has followed Pascher in using the terminal component *-phyta* in the place of *-phyceae* in the divisional names of the algae. Terminations derived from φῦκος not only have a precise meaning but are so old and well established in algological literature that their suppression in favor of the less precise *-phyta* is to be regretted. We thus have Chlorophyta (green plants), Phaeophyta (brown plants), Rhodophyta (red plants), instead of Chlorophyceae (green algae), Phaeophyceae (brown algae), and Rhodophyceae (red algae). If by adopting Pascher's terms we had arrived at a uniform terminal component for all divisions of plants, this might justify the *-phyta* ending. This is not achieved, however, since the fungi, gymnosperms and angiosperms were designated by Professor Smith at least as recently as 1938 as Eumycetae, Gymnospermae and Angiospermae, respectively. The divisional names in *-phyta* moreover lead to certain unnecessary inconsistencies in systematic arrangement. Thus the author recognizes a single class (Chlorophyceae) in the marine green algae, three classes (Isogeneratae, Heterogeneratae and Cyclosporeae) in the brown algae and one class (Rhodophyceae) with two subclasses (Bangioideae and Florideae) in the red algae. If one is to accept a class Chlorophyceae in the green algae and a class Rhodophyceae in the red algae, there would be equal justification for a single class Phaeophyceae in the brown algae. It would be futile to attempt to correlate the different categories of the various divisions of

algae. Nevertheless there is little ground for believing that the differences between the Bangioideae and Florideae in the Rhodophyceae are of lesser magnitude than those between the Isogeneratae, Heterogeneratae and Cyclosporeae in the Phaeophyceae, or that the three latter deserve the rank of class while the two former remain subclasses.

Similarly, little is to be gained by substituting Blakeslee's terms homothallic and heterothallic for the old and generally used terms monoecious and dioecious. Even isogamous algae usually show a physiological anisogamy and the male and female thalli can be separated on the basis of the different behavior of their gametes.

Probably in no other group of plants are details of the life history so intimately linked with classification as in the algae. Hence it does not seem out of place to consider briefly two instances of morphological interpretation in the brown algae to which the reviewer takes exception.

Owing to the extremely doubtful results of a few investigators in regard to the behavior of the zoids from the pleurilocular organs of *Ilea, Colpomenia* and *Scytosiphon* the author takes a noncommittal stand with reference to the nature of the macroscopic thalli in these genera. There seems to be little reason, however, for questioning their asexual or sporophytic character. If the plants were gametophytes and the zoids from the plurilocular organs gametes, it is to be expected that a generation forming unilocular sporangia, the seat of the reduction division in this group of brown algae, would be formed at some phase in the life cycle. Although these genera are found in many parts of the world and have been studied extensively both from field collections and in culture, they have never, as far as the reviewer is aware, been known to form unilocular sporangia. The evidence is overwhelmingly in favor of the conclusion that the thalli represent the sporophytic generation, that sexuality has been lost entirely in these genera, and that the plants reproduce themselves only by zoöspores from plurilocular sporangia.

The author refers to the eggs and sperms of the Fucales as macrospores and microspores, respectively. Although the evolutionary origin of the reproductive organs of the Fucales is still unknown, there is little justification for considering the eggs and sperms as the equivalent of spores. In the female sex organs meiosis is always followed by one series of mitotic divisions, resulting in the formation of eight haploid nuclei, while in the male organs meiosis is followed by four or five series of divisions, resulting in the formation of 64 or 128 nuclei. The contents of the mature reproductive organ may thus be looked upon, in the opinion of Strasburger, as a reduced gametophyte of which all the functional nuclei have become separated as gametes. According to this interpretation, which apparently is the one accepted by

the author, the four nuclei formed in consequence of meiosis would be the only equivalent of spores in the Fucales.

In the systematic arrangement and in the descriptions, the author has taken account of the many recent advances in our knowledge of the structure and reproduction of the algae. The green algae are classified according to the system previously published by the author while in the brown and red algae the systems of Kylin are adopted. The same general plan is followed with respect to the treatment of the three major groups. In each case the divisions are characterized and keys and descriptions are given to the classes, orders, families, genera and species. The authors and dates of publication of the genera are given as well as the more important references on their structure and reproduction. For the species, in addition to the description, the Monterey and Pacific Coast distributions are given, and where necessary remarks on the biology or other matters of a critical nature. The citations of literature for the species include those to the more important synonyms, the original description, and the combining author of the combination in the case of a transfer. The type locality is given separately.

The volume embraces 177 genera and 392 species and varieties. Several species are reported for the first time from this coast and the following are newly described: *Ralfsia pacifica* Hollenberg, *Desmarestia linearis* Gardner, *Porphyra Thuretii* Setchell and Dawson and *Herposiphonia pygmaea* Hollenberg. Several new combinations are made in the genera *Acrochaetium* and *Fosliella.* The combination *Acrochaetium Macounii* had, however, been made previously by Hamel (Rev. Alg. 3: 184. 1928).

In his treatment of *Acrochaetium* and *Rhodochorton* the author departs from the generally accepted concept of the limits of these genera. He places in *Acrochaetium* all the species of this complex which form only monosporangia as asexual reproductive organs and in *Rhodochorton* all those bearing tetrasporangia, irrespective of the fact that they may also form monosporangia, as is the case in *Rhodochorton* (*Acrochaetium*) *Daviesii,* and irrespective of the type of chromatophore. Other modern writers who recognize the two genera as distinct refer to *Acrochaetium* all species in which the cells contain from one to a few chromatophores, whether they be stellate, plate-like or band-shaped, and to *Rhodochorton* those species in which the cells contain from a few to many chromatophores. Accordingly *Rhodochorton* never includes species forming monosporangia. The limits between *Acrochaetium* and *Rhodochorton* admittedly are not sharp and a few workers have consequently accepted the conclusions of Drew, who maintains that the two genera should be united under the name *Rhodochorton.* In general, however, the two genera are readily separable on the basis of the type of chromatophore. According to the arrangement of the author there would be ample justification for uniting

them, since *Rhodochorton* would not only be composed of a heterogeneous assortment of species but would even include the type species of *Acrochaetium*, namely, *A. Daviesii.*

In accordance with accepted custom, the author recognizes a family Chantransiaceae, in which he places *Acrochaetium* and *Rhodochorton.* Since the genus *Chantransia* of De Candolle did not include a single species of *Acrochaetium* or of *Rhodochorton,* the family name Chantransiaceae is in contravention of Article 23 of the International Code (1935). The name was recently changed to Acrochaetiaceae by Fritsch (Bot. Rev. 10: 258, note. 1944).

The order Gelidiales is characterized as having cruciately or zonately divided tetrasporangia. However, as now recognized this order includes only genera with cruciately divided sporangia.

The family Nemastomaceae is characterized as having zonately divided tetrasporangia but when Kylin established the family he characterized it as having, as far as known, cruciately divided sporangia, which is true at least of two of the three genera, namely, *Nemastoma* and *Platoma.* Until recently sporangia were not known in the remaining genus, *Schizymenia.* In 1943 Smith and Hollenberg transferred to *Schizymenia* the *Peyssonneliopsis epiphytica* of Setchell and Lawson as well as its so-called host, which Smith and Hollenberg believed to be stages of one and the same plant. This species forms zonately divided tetrasporangia in nemathecia. In the present volume, tetrasporangia are reported for the first time in *Schizymenia pacifica* but no specific statement is made as to their method of division. The sporangia are, however, said to be remote from one another, which is also the condition in *Nemastoma* and *Platoma.* Sporangia are still unknown in the type species of *Schizymenia, S. Dubyi,* but their localization in nemathecia in *S. epiphytica* is a condition which is foreign to *Nemastoma* and *Platoma* as well as to *S. pacifica,* which has heretofore been considered a good species of *Schizymenia.* It would seem therefore that the condition in regard to the sporangia of *S. epiphytica* is sufficiently distinct from that in the other members of the Nemastomaceae to justify its exclusion from both *Schizymenia* and the Nemastomaceae.

A genus of particular interest is *Goniotrichopsis,* which was described by the author in 1943. This genus is closely related to *Goniotrichum* but differs from it and all other marine Bangioideae, as far as the reviewer is aware, in one significant feature, namely, the presence in each cell of several disc-shaped chromatophores. This is a condition which should be sought for in other members of the Bangioideae.

Tetrasporangia are reported in *Opuntiella.* This is an important discovery inasmuch as sporangia had thus far not been recorded for this genus.

The comprehensive keys to the genera have passed through

four revisions in the course of Professor Smith's seventeen years' study and teaching at the Hopkins Marine Station. The rigorous tests which they have consequently undergone coupled with the fact that they are based almost exclusively on vegetative characters are good guarantees of their great value.

The illustrations, many of which were prepared by Mrs. Carl F. Janish, rank amongst the best that have been given of the algae. Approximately 80 per cent of the species are illustrated, many of them for the first time. The drawings show the general appearance of the plant but details of structure are also figured if necessary in the identification of genera or species.

Students of marine algae throughout the world will welcome this volume. The work may well serve as a guide in the preparation of future marine floras.—George F. Papenfuss, Department of Botany, University of California, Berkeley.

*Illustrated Flora of the Pacific States.* Volume two. *Buckwheats to Kramerias.* By LeRoy Abrams. Pp. viii + 635, with 1663 figs. Stanford University Press. 1944. $7.50.

Volume two of this important work embraces those families from Polygonaceae through Krameriaceae. As in volume one the species, with very few exceptions, are illustrated, but unlike the preceding volume the illustrations are aggregated on separate pages, thus reducing costs and greatly enhancing the appearance of the format. The quality of the illustrations is much improved and greater attention has been paid to the depiction of significant details.

The treatment of families follows the author's established policy of segregation; thus we find instead of the single family, Leguminosae, the families Caesalpinaceae, Mimosaceae and Fabaceae. The Rosaceae and Saxifragaceae of other California authors receives similar treatment, a point of view that can be easily and logically defended. Certain inconsistencies in this policy stand out with respect to some of the smaller families. Aizoaceae includes two somewhat discordant elements, the Molluginaceae having hypogynous flowers and a curved embryo much like that found in the Caryophyllaceae, and the Ficoidaceae with its epigynous or perigynous flowers and an embryo that in most cases is bent much like that in many Cactaceae. Cabombaceae with its ranalian type of flower is included with the Nymphaceae, a group having many features allying it with the Rhoedales. These are minor problems and the urge to split these families certainly does not have behind it the impelling force of "facility in handling" that one finds in such large families as Leguminosae and Rosaceae.

A similar policy is adhered to in the treatment of genera, for example, it seems good judgment to separate *Grossularia* from *Ribes* and *Fendlerella* from *Whipplea.* The number of "problem

genera" treated in volume two is outstanding. It was no easy task to arrive at decisions in such genera as *Chorizanthe, Eriogonum, Atriplex, Montia, Lewisia, Silene, Ranunculus, Delphinium,* almost the entire Cruciferae, *Dudleya,* the *Potentilleae, Lupinus, Trifolium, Astragalus* and *Hosackia.* To be sure, the treatments of some of these genera were contributed by specialists and others followed the works of specialists, but the genetic difficulties inherent in many of them would seem to defy rationalization in the light of the present state of our knowledge about them.

To some, the subspecific categories appearing in the work might seem a bit confusing since both of the terms "subspecies" and "variety" are used. In many genera the category subspecies is used while in others the category variety is used, and in others both categories appear. I suspect that this is not intended to indicate their arrangement in the order outlined for these categories in the International Rules but rather is evidence of the conservative policy of the author in avoiding, in a work of this type, the making of changes and new combinations except where necessitated by a change in status of the entity. The author is to be congratulated for this point of view. When a new combination is unavoidable, the subspecies category is utilized.

Each species is given a common name and in general these are perfectly good English or early Californian vernacular. The tendency among laymen to use the generic name with a vernacular adjective is given recognition with a euphonius and dignified result. This is a subtle way of overcoming the layman's horror of scientific names. It is gratifying to see that where it is necessary or desirable to combine words a hyphen is used in accordance with good grammatical custom.

During the long interval that the volume was in press many entities in the area treated had been described as new and the concepts of others had been revised. These are mentioned, with their bibliographic reference, in the appendix at the end of the volume. Here, a count on the genus *Lupinus* reads like a tally sheet in a three-cornered race between Smith, Heller, and Eastwood. The score to date is Eastwood 45, Smith 22, and Heller 10.

The appearance of volume two further increases the desire to receive volumes three and four and thus bring to completion a work of which we are all justly proud.—Herbert L. Mason, Department of Botany, University of California, Berkeley.